1947

Extent and causes of variability in Clinton Oats

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NOTE TO USERS

EXTENT AND CAUSES OF VARIABILITY IN CLINTON OATS

by

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A Thesis Submitted to the Graduate Faculty
for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject: Crop Breeding

Approved:

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Iowa State College

1947

TABLE OF CONTENTS

INTRODUCTION

Clinton oats were grown on approximately 750,000 acres in 1947. The estimated acreage for 1948 is 15,000,000 acres. Since Clinton (and many other selections from crosses with Bond) is resistant to Helminthosporium victoriae Meehan and Murphy, the serious disease which is so destructive to varieties originating from crosses with Victoria, its increase in the corn belt is expected to be rapid. Clinton, Mindo, Benton, Bonda, Bonham, Eaton, Mohawk, Advance, Zephyr, Andrew, Shelby, Sac and other varieties derived from Bond crosses are expected to replace the acreage formerly planted to Boone, Tama, Osage, Neosho, Control, Vicland, Vikota, Cedar, Forvic and other Victoria derivatives.

Clinton oats have a rather wide adaptation, excellent strength of straw, high yield and high test weight. This variety is resistant to the races of stem rust commonly found in the United States. It is not resistant to all races of smut, but has generally exhibited good field resistance in the corn belt. Clinton is resistant to nearly all races of crown rust. Race 45 and similar races attack Clinton, although they often appear so late in the season that they cause little damage.

Clinton has a very large number of desirable agronomic and pathologic characteristics, in common with many selections obtained from Bond crosses, However, Clinton has repeatedly given rise to a wide variety of offtypes. Although these offtypes apparently have not reduced the economic value of Clinton they have caused considerable concern in the maintenance of certifiable seed.

Before considering this problem of variability in Clinton it will be desirable to retrace the main steps in its production and introduction. Clinton oats resulted from a species cross between D69, an unnamed selection from a cross between varieties of Avena sativa L., and Bond, a variety of Avena byzantina C. Koch. The D69 parent originated from a Richland x Green Russian cross made at the Iowa station. D69 is resistant to stem rust Puccinia graminis avenae Erikss. and Henn. Bond, a selection from a cross of Red Algerian x Golden Rain, was introduced from Australia and was discovered to have good resistance to crown rust Puccinia coronata Corda., loose smut Ustilago avenae (Pers.) Rostr. and covered smut Ustilago kolleri Wille.

The cross D69 x Bond, from which Clinton and several other varieties have been selected, was made by Dr. H. C. Murphy in 1932 at Ames, Iowa. From a series of panicle rows in the F_6 generation one line (1335-3) proved to be highly disease resistant, and showed excellent standing ability. The C.I. number 3971 was assigned to this oat by Dr. T. R. Stanton of the Division of Cereal Crops and Diseases, U. S. Department of Agriculture.

In 1943 a total of 680 panicle rows of C.I. 3971 were grown on the Agronomy Farm at Ames, Iowa, for purification and increase. About 500 rows were considered sufficiently uniform to bulk for the initial increase. In October, 1943, twenty-five pounds of the bulked seed were planted at Mesa, Arizona. Seed from the Arizona winter crop was immediately shipped to Aberdeen, Idaho, where 67 bushels were planted in May, 1944. Under irrigation at Aberdeen, Idaho, the Clinton seed was increased to 1,207

bushels. This seed was shipped to Iowa for distribution in the fall of 1944. A plan for the distribution was worked out by representatives from the Iowa, Indiana and Illinois Experiment Stations.

Murphy (35, p. 6) described the naming of Clinton oats as follows:

> The name Clinton was proposed and approved by an informal conference of representatives of the Iowa, Indiana and Illinois Experiment Stations and the United States Department of Agriculture, meeting in Cincinnati, Ohio, November 11, 1943. The name recognizes the counties of Clinton in Iowa, Illinois and Indiana.

Plant breeders at several different stations observed the variability in height and maturity of Clinton. At first it was supposed that variability was due to bulking of progeny plants before the line had become homozygous. Reselection in later generations, however, failed to fix the Clinton type into a uniform variety. Other possible explanations for the offtype plants were advanced; such as natural crossing with other varieties, mechanical mixing during planting and harvesting, and cytological instability. Regardless of the mechanism giving rise to variation within the Clinton population, the offtype plants continued to increase and trouble was encountered when large fields were inspected for certification.

From the standpoint of field inspection and certification it was deemed desirable to produce, if possible, a more uniform reselection of Clinton oats. At the same time some fundamental information on the causes of variability in oats might also be obtained. Therefore, this study of variability in Clinton oats has taken two paths; one has been an attempt to select a true breeding Clinton variety without mutant forms, and the other to study the mutant forms and learn their causes.

REVIEW OF LITERATURE

The pure line concept in small grain breeding

The pure line concept has been important in our reasoning about self pollinated plants since it was introduced by Johannsen in 1903. Since this date many experiments have been conducted to study selection within pure lines of self pollinated crop plants.

Fruwirth (17) tested the pure line theory with several self pollinated crops. Fichtel Mountain oats were used in one of his experiments. He selected in two directions simultaneously; one direction (plus) was for more hairs on the callus of the grain, and the other (minus) was for fewer hairs. After nine years of selection he was unable to show any significant differences in the number of hairs on the callus of the plus and the minus selections. In the same length of time he was not able to change by selection the percentage of spikelets containing two kernels. Fruwirth (17, p. 94), concluded that,

> Critical scientists may, perhaps, object that if these various experiments had been continued much longer, some hereditary effects would be produced. In such a case, I admit that changes could occur; but I am of the opinion that they would not be the effects of selection. They would be mere spontaneous variations (mutations) whose production would be wholly independent of the selection; but whose preservation would naturally be the result of selection.

Hayes and Immer (22) reported no differences in yielding ability among pure lines of Victory oats, although many minor variations of a heritable nature were observed.

Natural crossing in oats

Stanton and Coffman (45) were the first to conduct a well planned experiment to measure the amount of natural crossing in oats. White glumed varieties were planted next to black glumed varieties having similar flowering dates. Using the character black glumes as a dominant genetic marker, they showed that oat varieties of the species Avena sativa crossed an average of 0.36 percent in 1922 at Akron, Colorado. They demonstrated in the same experiment that certain varieties, such as Iowar with 0.97 percent natural crossing, were much more subject to crossing than varieties such as Pringle Progress with only 0.10 percent natural crossing. Other investigators have since noted great differences among varieties in their tendency to cross pollinate in nature.

From 1920 to 1922 Griffee and Hayes (20) conducted experiments at St. Paul, Minnesota, to measure the amount of natural crossing in certain oat varieties. Their methods were similar to the ones previously mentioned in which black and white glumed varieties were grown in adjacent rows. Any black glumed plants which appeared in the white glumed varieties the following season were considered natural crosses. Kanota, a variety belonging to the species A. byzantina, gave the highest amount of natural crossing with 1.4 percent. Victory, belonging to A. sativa, gave the lowest amount with only 0.04 percent natural crossing.

Studies by Garber and Quisenberry (18) from 1922 to 1925 at Morgantown, West Virginia, indicated that A. byzantina var. Fulghum was

much more subject to natural crossing than the varieties of A. sativa tested. The authors also believed that natural crossing in oats was favored more by dry weather than by rainy weather.

Other studies at Morgantown by Hoover and Snyder (24) gave an average of 0.41 percent natural crossing in Fulghum oats for three years while A. sativa varieties averaged only 0.013 percent in the same period of time. Hoover and Snyder also gave evidence that more natural crossing occurred in the secondary florets of oats spikelets, but they gave no reason for this phenomenon.

In small grain natural crossing experiments at Saskatoon, Saskatchewan, from 1925 to 1929, Harrington (21) found hulled oats to cross an average of 0.07 percent. The hulless variety Liberty gave as high as 9.82 percent natural crossing and averaged 3.68 percent during the five years of testing. There seemed to be no relation between seasonal conditions at Saskatoon and the amount of natural crossing in oats.

In 1930 and 1931 Derick (12) obtained 0.10 percent natural crossing between A. sativa and A. fatua. He also conducted an experiment to determine how far oat pollen could be carried by wind and still function. He found that pollen was carried at least as far as four feet under the conditions in Ottawa, Canada.

Coffman and Wiebe (9) have shown that the wind can carry viable oat pollen at least as far as ten feet to facilitate cross pollination. This distance is probably not the maximum possible for cross pollination

in oats, but no experiments have measured natural crossing at a greater distance, to the writer's knowledge.

Jones (29), in Wales, tested natural crossing in oats and used the "mixed seed" method not heretofore described. He planted equal weights of black and white seeds in the same row in order to get the pollen even closer to the flowers than possible when using the alternate row method used by other investigators. However, under conditions in Wales, he was unable to show differences in natural crossing between the "mixed seed" rows and the alternate rows. Jones found that early varieties gave more natural crossing than late varieties. Over a five year period using several varieties from five different species he obtained an average of only 0.07$\frac{1}{4}$ percent natural crossing.

Variability in oats

One of the first extensive investigations of variability in oats in this country was reported for the Burt variety by Coffman, et al. (7). Burt is generally considered to belong to A. byzantina, a species which is noted for its variability. The authors studied several morphological characters of the grain and concluded that the Burt variety was far more variable than was previously realized.

A similar study of Kherson oats, A. sativa, was made by Coffman and Stanton (8). They were able to select many different types from Kherson. The variety was found to vary for several plant characters, disease reaction, and grain characters.

Oat literature includes many accounts of fatuoids, or false wild oats. Stanton, et al. (46) reported the variability occurring in Fulghum oats, principally due to the spontaneous appearance of fatuoid types. Huskins (26) has recently reviewed the literature and brought the fatuoid and speltoid problems up to date.

Oat cytology

Stanton (47) has reviewed the work of various cytologists working with oats prior to 1936 and classified oats into three groups on the basis of their chromosome numbers.

Group I — 7 haploid chromosomes

Avena brevis Roth
" *wiestii* Steudel
" *strigosa* Schreb.
" *nudibrevis* Vav.

Group II — 14 haploid chromosomes

Avena barbata Pott
" *abyssinica* Hochst.

Group III — 21 haploid chromosomes

Avena fatua L.
" *sativa* L.
" " *orientalis* Schreb.
" *nuda* L.
" *sterilis* L.
" " *ludoviciana* Dur.
" *byzantina* C. Koch
" *sterilis algeriensis* Trabut

Crosses between 21 x 21 chromosome oats are completely fertile and generally show very little irregularity, but crosses involving unequal chromosome numbers are nearly always extremely nonfertile (1, 10).

The literature on the cytology of oats is rather incomplete and indicates that much research is yet to be accomplished. However, some interesting and worthwhile studies have been made of particular phases of oat cytology. The cytology of fatuoids has been reported by several workers from Japan, Europe, Canada and this country. Because these studies will not be reviewed in detail here, the reader is referred for a more complete summary to the recent report by Huskins (26) on the subject of fatuoids.

The cytology of aberrant albino mutants in an F_4 oat cross was described by Philp (38). He reported green plants with 41 chromosomes and albino plants with only 40 chromosomes. Chromosome loss followed abnormal chromosome pairing, or allosyndesis. Micronuclei were frequently observed in this material, as were univalent chromosomes, lagging, and splitting of univalent chromosomes at anaphase I.

Philp (39) also reported on the cytology of aberrant leaf width in a cross of A. sativa gigantica L. and A. fatua. As in his previous study he found that the changes could be ascribed to loss of a whole chromosome. Seedlings whose leaf widths were less than 3 mm. had 40 chromosomes and the wider leaved plants had 41 chromosomes. Philp found the 40 chromosome plants to be much less vigorous than the ones with more chromosomes, indicating that oat plants need their complete chromosome complement for normal growth.

Longley and Stanton (32) made a cytological analysis of five dwarf types of oats and found 21 bivalent chromosomes at diakinesis in all

dwarf forms. One or more pairs of chromosomes sometimes failed to be included in the metaphase plate, but an abnormal environment at collecting time was thought to be the reason.

Church (6) studied the cytology of Avena sativa var. Mutica and described several outstanding irregularities. Lagging bivalents and univalents were found in anaphase I. Occasionally extreme lagging and extrusion was noted at telophase II. Church states (6, p. 612),

> The homotypic telophase is marked by extrusions closely aggregated about the nuclei, which result in a high degree of polycary in the tetrads. The normal pollen is in surprising contrast to such conditions in the maturation divisions.

Nishiyama (36), in Japan, has done much detailed work on the cytology and genetics of fatuoids, species crosses and other cytological investigations with oats. He studied A. sativa (varieties Banner and Kanota) and A. fatua pollen mother cells in detail and concluded that there was very little irregularity at meiosis in these two species. About the hybrids of A. sativa x A. fatua, Nishiyama (36, p. 96) had this to say,

> In Avena species the meiotic behavior of chromosomes is held in harmony, and the conjugation of the homologous chromosomes is regularly carried out. While in the hybrid, the cytological harmony is more or less disturbed, and occasionally the conjugation occurs abnormally between semi-homologous chromosomes from different genomes.

Philp (37) studied hybrids between A. sativa and A. fatua both genetically and cytologically. He found the parents to behave regularly at meiosis. One or two bivalents or univalents were often found to lie off the metaphase plate in the hybrid material. At

anaphase I the univalents often lagged and split homotypically. At anaphase II they passed undivided and at random to the poles. Philp concluded that A. fatua chromosomes are mostly homologous with A. sativa chromosomes, but since univalents do occur, a few pairs are not completely homologous. He also believed that certain chromosomes within each haploid complement of each species were somewhat homologous with each other. This was shown by certain quadrivalent and trivalent associations found in the hybrids. Ellison (14) reported heteromorphic bivalent chromosomes at metaphase I in F_1 plants of A. strigosa hirtula Schreb. x A. brevis, both with 14 somatic chromosomes.

Love (33) has shown fine photomicrographs of heteromorphic bivalents in some offtype winter wheats. Upcott (51) has reported that in Tulip inverted segments which have also been translocated may show asymmetrical bivalents at metaphase I, and then a bridge and fragment at anaphase I. There is little indication in the literature to date that heteromorphic pairs of chromosomes are an important source of variability in Avena species.

Because of the importance of inversions to the present problem in oats variability, a few pertinent papers will be reviewed here. Richardson (42) gives a clear explanation of the consequences of crossing-over in structurally differentiated bivalent chromosomes. She has classified inversions into two main groups; those which do not include the centromere, and those which do include the centromere. When the centromere is not included in the inverted region and a single cross-over takes place in this

region, an acentric fragment, a dicentric bridge and two normal chromatids are formed at anaphase I. Crossing-over within an inversion which includes the centromere will result in free disjunction at anaphase I.

A chromatid bridge and fragment (fragment often not seen) at anaphase I is an indication that the plant under investigation contains pairs of chromosomes which are heterozygous for one or more inverted segments, usually on an arm of the chromosome away from the centromere (11, 13, 25, 30, 34, 39, 41, 48, 50).

An interesting paper by Howard (25) on meiotic instability in crosses between spring x winter oats has recently appeared. Picton, a new winter oat in England, is the result of a cross of Argentine (spring) x Grey Winter. It was found that Picton was quite variable; producing chlorotic plants and late flowering offtypes. Cytological examination of some sporocytes revealed that both univalent chromosomes and bridges with fragments were rather frequent in this variety. When the cross was remade, however, no bridges could be discovered in the F_1 plants. Spring x spring oat crosses gave only 1 percent of univalents, and the same was true of winter x winter crosses; but spring x winter crosses gave 20 percent univalents. Howard explains that pairing between chromosomes from different genomes may be the answer to this irregularity in Picton oats. The spring and winter type chromosomes seem to be only partially homologous.

Kostoff (31) studied meiosis in a species hybrid of Helianthus tuberosus L. x H. annuus L. and found that the F_1 plants were heterozygous for at least five different inversions. Geitler (19) found an exceedingly high number of inversions in Paris quadrifolia L.

Emsweller and Jones (15, p. 76) working with an Allium species hybrid found many bridges, fragments and peculiar interlocking chromatids. They state,

> There is, however, some evidence in this hybrid that bridges also arise when inversions are probably not concerned. When two chromosomes pair in such a manner that their insertion regions are not opposite each other, and a single cross-over occurs in the interval between the insertions, a bridge will ordinarily result. . . . The situation is probably brought about, therefore, more as a positional effect of homologous sectors rather than as simple inversions. . . . It seems more likely that bridges arise in a number of ways from unusual crossing-over. Some of the causes may be translocations, or simple rearrangements of insertions as well as inversions.

Unusual "position effects" may be produced when translocations, deletions or duplications take place in the chromosome complement of an individual. When neighboring portions of chromosomes are taken away and replaced by other portions sometimes changes known as "position effects" are noted in the phenotype. Catcheside (4) described this condition in Oenothera and others have described it in animals.

Somatic segregation

A simple and usable definition of somatic segregation has been given by Chittenden (5, p. 357). He says,

> "Somatic segregation may be defined as the production of two genetically dissimilar cells at a somatic cell division."

Countless fruits, flowers and crop plants showing parts which vary in color or morphology on the same plant have been described in the past. Several explanations have been advanced to account for these spontaneous

vegetative changes which occur in somatic tissue after fertilization has taken place. Deletions of a part of a chromosome may explain certain vegetative changes which take place in plants. Somatic crossing-over has been strongly suggested as the mechanism for somatic segregation in several crop plants (28). Stern (49) has demonstrated that somatic crossing-over can occur in Drosophila melanogaster. Translocations involving two or more chromosomes may cause mosaic patterns to appear in plants. Non-disjunction of one or more chromosome pairs may be another reason for somatic variation.

Jones (27), using aleurone and endosperm colors in maize, studied the frequency and nature of paired mosaics. The mosaics appeared as small twin spots, one being lighter in color and the other darker than the surrounding tissue. Unequal mitosis was used to explain the changes in color of the somatic tissue. If both spots of the twin spots are considered to be derived from a single cell, then the light colored spot is due to an absence of the color allele, while the dark colored spot received a double dose of the color allele. The daughter cells which produce the twin spots are thus somatically unbalanced in relation to the rest of the somatic tissue.

Several instances of chimeras or bud-sports have been reported in small grains. Åkerman (3) found a spike of beardless wheat which was differentiated longitudinally into two distinct types. One-half of the spike had the speltoid features of upright glumes which were tightly pressed against the rachis, while the other half of the spike was like normal beardless wheat. He explained this peculiar spike, and other

similar ones discovered later, as being due to a loss mutation in somatic tissue early in the formation of the spike. All seeds from chimeric wheat spikes gave rise to plants of normal type only. The speltoid parts were from epidermal tissue which did not produce gametes, hence only normal progeny resulted.

Hedayetulla and Sen (23) recently reported bud mutations in paddy, where tillers from the same rice plant gave very different progeny.

Pridham (40) in Australia, found a chimeric oat plant in which the panicles were hulless with multiple florets in the top, and hulled with only paired florets at the base of the panicle. Several other chimeric oat plants have been found in Germany, England, Canada and the United States and these have recently been reviewed by Huskins (26).

The use of X-ray irradiation upon oat grains and seedlings has shed some light upon the nature and rates of chromosome aberrations in Avena. Stadler (44) found a higher mutation rate among oats species with seven and fourteen haploid chromosomes than among the higher polyploid series. This would indicate that much duplication of chromatin material has taken place in the phylogeny of hexaploid oat species.

By using heavy X-ray dosages upon dry oat seeds Fröir (16) obtained some interesting chlorophyll mutations. He found that with X_1 plants (first generation after treatment) the sterility was very pronounced. Besides many chlorophyll deficient plants in hexaploid oats he obtained other mutant types. He states (16, p. 377).

As regards other morphological and physiological mutations in X_2, the hexaploid oats have distinctly responded to the 10.000-r treatment with a great many genomatic rearrangements, leading to segregations of new types, varying in length of straw, tillering capacity, earliness, leaf width, hairiness of nodes, etc.

MATERIALS AND METHODS

Natural crossing experiments

Seven black glumed varieties of medium to early maturity were obtained from Dr. T. R. Stanton, Division of Cereal Crops and Diseases, U. S. Department of Agriculture. These varieties were Black Mesdag, Joanette, Early Joanette, Fulmer, Awnless Monarch, North Finnish and Old Island Black.

A number of trial combinations were made between the black glumed varieties and certain white glumed varieties in 1945. Notes were taken on the dates of flowering, so that better matching of flowering dates of varieties could be accomplished in the 1946 season.

The natural crossing blocks or plots were laid out so that crossing could be measured between plants within a row, as well as between plants in adjacent rows. The light glumed varieties Clinton, Mindo, Benton and Boone were grown with the black glumed varieties mentioned above. In one case equal quantities of seed of white and black glumed varieties of similar maturity were mixed together and planted in the same rod row. This planting constituted the mixed row test. In the next series adjacent rod rows of each of the white and black glumed varieties were planted one foot apart. This constituted the adjacent row test for natural crossing.

By picking at random from 50 to 100 white glumed panicles from each row for progeny testing the following season, natural crossing percentages could be determined. The panicle rows of the light colored varieties were

grown in rows four feet long, with one foot distance between the rows. The short rows served a double purpose. Since the Clinton panicles were picked from the population at random, they also were used for recording the variability of this variety. Variability was measured by counting the Clinton offtype rows from the natural crossing plots. At maturity all individual plants from panicle rows were pulled and the number of white and black glumed plants (F_2) recorded. Data on the variability within the varieties Mindo and Benton also were obtained by counting the offtype panicle rows before they were pulled for natural crossing counts.

Testing for mechanical mixtures

One of the possible reasons suggested for the variability in Clinton oats has been mechanical mixing with other varieties during planting, harvesting and threshing. Observations were made on the possible amount of mixture obtained by planting with V-belt planters, funnel type planters and various other methods of planting small grains.

The most reliable test of mechanical mixing was recorded for the rod row thresher. The method of testing for mixtures was simple and quite effective. Several white glumed oats bundles were threshed first and then a change was made to bundles of black glumed oats. By alternating white and black glumed oats and counting the off-colored grains in each sample of seed a good indication of the amount of mixing from sample to sample was obtained.

Study of tillers from individual plants

As early as 1944 it had been suspected that different panicles (tillers) from the same individual Clinton plant might not always produce identical progenies. Since this phenomenon was in direct contradiction to the pure line concept, and to genetic principles in general, tests were conducted to make certain whether or not tiller differences did occur on individual Clinton plants.

Spaced plants were pulled, their roots were washed and a careful examination made to be sure they were single plants. The panicles from each plant were then planted in adjacent panicle rows the following season and observed for differences in date of heading, height, disease reaction and panicle type. It was frequently possible to make a photographic record of differences in tiller progeny coming from the same plant.

Progeny testing of Clinton families

This study of variability in Clinton oats had its beginning when 50 panicles representing the typical Clinton type were picked from an increase field at Aberdeen, Idaho, in August, 1944. While roguing the increase fields in Idaho, the writer and others also collected many offtype plants from the Clinton variety.

In 1945 the 50 panicles were planted in individual rows each four feet in length. About 150 progeny rows of various offtype Clinton plants also were grown. Variability within and between these rows was recorded.

Fifty panicles from each of 40 apparently uniform Clinton type rows were harvested for further pedigree testing the following year.

In 1946 50 panicle rows were grown to test the breeding behavior of each of 40 progenies saved in 1945; making a total of 2,000 rows. Each of these 50 row progeny tests was called one family, because it traced back to one panicle from Aberdeen, Idaho. Records were kept for variability within and between these families on the following characters:

Stem rust	Strength of straw	Tillering ability
Crown rust	Leaf width	Panicle type
Hale blight	Color and bloom of foliage	Plant height
Smut	Color of grain	Date of heading

Clinton yield test

In 1947 a rod row yield test was grown to determine the yielding ability, disease resistance, grain quality and general uniformity of some selected Clinton families. There were 26 families (entries) from Ames, each consisting of five separate progeny rows, 9 from Aberdeen, Idaho, and Clinton itself was used as a check. This made a test with a total of 36 entries.

A 6 x 6 triple lattice design was used in this yield test. Each entry was replicated six times. Each plot consisted of five sub-plots representing the strains within a family. All five of the rows from each plot were harvested and threshed separately. This experiment had a total of 1,080 rows planted under good conditions, in medium fertile Clarion silt loam soil at the Agronomy Farm, Ames, Iowa.

Cytological methods

Cytological studies were made on F_1 plants of D69 x Bond (the original cross from which Clinton was selected), of the Bond and D69 parents, progenies of offtype plants, and progenies of Clinton type plants. The cytological examination was undertaken using the aceto-carmine smear method on young anthers, as recently reviewed by Smith (43).

Whole panicles were killed in 3 parts absolute ethyl alcohol to 1 part glacial acetic acid. After two or three days this solution was drained off and replaced by 70 percent ethyl alcohol. The bottles containing the single panicles were then placed in cold storage at about 40° F. until the smears were made.

Smears of oat anthers were made in the following manner: Three anthers were taken out of the primary floret by means of iron needles. Two of the anthers were held back in a watch glass in 45 percent acetic acid while the first was being examined for its meiotic chromosomes. With one anther on the slide, one or two drops of acetocarmine were sufficient to keep the anther from drying while it was being cut into several smaller pieces. With a spear-point needle, using a rocking motion, the sporocytes were forced from the pieces of anther. As much anther debris as possible was removed from the slide. More acetocarmine was added as needed during these manipulations to keep the sporocytes from drying out. Rapid examination under low magnification was sufficient for judging the meiotic stages.

If the chromosomes were considered to be in the proper stage, the preparation was covered with a clean cover glass. The slide was passed several times through an alcohol flame, until it was quite warm to the touch. After allowing the slide to cool for a few moments a blotter was placed over the cover glass and considerable pressure was applied with the thumb. The slide could then be observed for from a few minutes to an hour or more under higher magnification without danger of drying. The better slides were temporarily sealed around the edges with wax, for further study or photography. The two reserve anthers from desired florets were often smeared to obtain additional data. Much time was spent in attempting to make oat smears permanent, but it proved not to be worth while.

A binocular Bausch and Lomb microscope was used for all chromosome observations. The photomicrographs were taken with a Leitz "Makam" camera. A 10X ocular and 40X oil immersion objective were used for photographing chromosomes, giving a magnification of 400X on the original negative. Magnifications of 800X were then obtained by enlarging the original photomicrograph 2 times.

EXPERIMENTAL RESULTS

Natural crossing experiments

The percentages of natural crossing in oats which occurred at two Iowa locations for two seasons are shown in Tables 1 to 4, inclusive. Selections from crosses with Bond included Benton, Clinton and Mindo. Boone was planted to test its natural crossing but most of the plants were destroyed by Helminthosporium victoriae.

Table 1. Frequency of natural crossing between Clinton and black glumed oat varieties grown at Ames, 1945.

1945 row number	Varieties	Number panicle rows 1946	Number of plants: White glumes	Number of plants: Black glumes	Percent crossing
1412	Clinton (alone)*	50	1,513	4	0.26
1413	Clinton-Black Mesdag	50	1,237	5	0.40
1414	Clinton (alone)	50	1,401	3	0.21
1416	Clinton (alone)	25	681	2	0.29
1417	Clinton-Awnless Monarch	25	622	1	0.16
1418	Clinton (alone)	50	1,440	8	0.55
1420	Clinton (alone)	50	1,365	2	0.15
1421	Clinton-Fulmer	50	1,573	3	0.19
1422	Clinton (alone)	50	1,595	0	0.00
1426	Clinton (alone)	55	1,727	3	0.17

* Clinton (alone) refers to Clinton grown in a row adjacent to black glumed oats.

Table 2. Frequency of natural crossing between Clinton, Benton and Mindo and Black glumed varieties grown at Ames, 1946.

1946 row number	Varieties	Number panicle rows 1947	Number of plants: White glumes	Number of plants: Black glumes	Percent crossing
2751	Clinton (alone)	65	1,767	3	0.17
2752	Clinton-Black Mesdag	55	1,461	6	0.41
2753	Mindo-Early Jeanette	60	1,370	20	1.44
2754	Clinton-Fulmer	80	1,824	10	0.55
2755	Clinton-Awnless Monarch	60	1,332	4	0.30
2756	Clinton (alone)	60	1,614	3	0.19
2757	Benton-Black Mesdag	70	1,429	5	0.35

Table 3. Frequency of natural crossing between Clinton and black glumed oat varieties grown at Kanawha, 1945.

1945 row number	Varieties	Number panicle rows 1946	Number of plants: White glumes	Number of plants: Black glumes	Percent crossing
7	Clinton (alone)	50	1,576	3	0.19
8	Clinton-Black Mesdag	50	1,793	3	0.17
9	Clinton (alone)	50	1,597	8	0.50
10	Clinton-Fulmer	50	1,735	1	0.06
11	Clinton (alone)	50	1,841	0	0.00

Table 4. Frequency of natural crossing between Clinton, Benton and Mindo and black glumed varieties grown at Kanawha, 1946.

1946 row number	Varieties	Number panicle rows 1947	Number of plants White glumes	Number of plants Black glumes	Percent crossing
1	Clinton (alone)	60	1,585	5	0.32
2	Clinton-Black Mesdag	40	1,348	5	0.37
3	Mindo-Early Joanette	50	1,310	60	4.38
4	Clinton-Fulmer	50	1,487	3	0.20
5	Clinton-Awnless Monarch	40	1,043	3	0.29
6	Clinton (alone)	30	924	1	0.11
8	Benton-Black Mesdag	50	1,432	0	0.00

Mindo, when grown in a mixture with Early Joanette, gave the highest amount of natural crossing at both Ames and Kanawha. There are several probable reasons for this high percentage of natural crossing. Mindo and Early Joanette both are early varieties which flower at the same time. Because their heights are similar the panicles are together when pollination takes place, making it possible for Early Joanette pollen to be on the same level as Mindo stigmas, or even above in some regions of the panicle. Oat pollen is heavy and falls rapidly, although it may drift slightly on a windy day. A short variety such as Mindo, therefore, may be in a more favorable position for cross pollination than a tall variety such as Benton.

The Benton variety was subject to very little natural crossing in these tests. Benton was taller than most of the black varieties. It was difficult to find a black glumed variety of similar height. A more refined

test, using statistical methods would be necessary to show that Benton actually is genetically or physiologically less subject to natural crossing than the other varieties. However, under the conditions of these experiments Benton showed the lowest percentage of natural crossing.

Clinton showed a moderate amount of natural crossing rather consistently at both Ames and Kanawha, Iowa. Its flowering time matched fairly well with Black Mesdag and Fulmer. Since Clinton plants averaged about four inches shorter than Benton, this placed the Clinton stigmas more nearly on a level with the pollen of the black glumed varieties and gave maximum opportunity for natural crossing. In two years, at two Iowa locations, Clinton averaged .25 percent of natural crossing.

It seems probable that oat varieties differ in their inherent tendency to cross pollinate, but this may not have been adequately tested. Critical tests must be used where all factors are controlled. Black glumes have been used almost universally as a tester for natural crossing. The differences in height of plants, their dates of flowering and other factors may have upset nearly all of the tests where varietal differences have been reported.

It has been suggested that differential disease reaction of closely related lines might be a better method of measuring natural crossing. In this way height and flowering differences would be at a minimum. For example, a pure line similar to Bond, except for resistance to stem rust, might be planted adjacent to Bond which is susceptible. Because

resistance is dominant, resistant plants from Bond seed would indicate that cross pollination had taken place the previous season. Large populations could be readily tested in the seedling stage in the greenhouse.

Although the Bond variety was not included in this phase of the study, it is known to be quite subject to natural crossing in the field. From 150 panicle rows of Bond grown in the 1947 nursery several plants were observed to be free of stem rust. This is a strong indication that natural crossing occurred between Bond and Clinton, because these two varieties were in close proximity to each other the previous season.

There was slightly more natural crossing in the mixed rows of black and white glumed oats than there was in the adjacent rows. An exception to this trend was observed at Kanawha in 1945, where more crossing took place, on the average, in adjacent rows than within the mixed rows. In general, the greater the concentration of foreign pollen the greater the chances for natural crossing, especially if the foreign pollen is at the same level or slightly above the stigmas of the tester variety.

A total of 41,798 oat plants were counted in 1946 and 1947, of which 174 plants were black glumed, making an average of 0.416 percent natural crossing for 1945 and 1946.

Testing for mechanical mixtures

At maturity varietal mixtures could sometimes be identified among Clinton families, while at other times these identifications were of a doubtful nature because of their resemblence to tall type mutants from

Clinton. Two hulless types were found in a Clinton field and were undoubtedly due to mechanical mixing. Other common varieties could often be identified with reasonable surety. Tests of the rod row thresher and the V-belt planters used at the Iowa station indicated that mechanical mixtures were occurring at an alarming rate.

The rubber V-belt on the planters carried oat grains under the belt to a wooden platform on practically every three row plot which was planted. Grains were then frequently seen to fall from the wooden platform into the furrows of the next plot. Considerable mixing was undoubtedly caused in the experimental plots by the use of the V-belt planters. New funnel type planters are now being used which are practically free of any possible mechanical mixing of seed at planting time.

The modified Vogel[1] rod row thresher used in the small grain nursery projects was found to be a frequent cause of mixing different varieties. A straw carrier and shaker made this machine undesirable for threshing rod row material where seed was to be saved for planting from year to year. For example, in one test to determine the prevalence of mixtures after flax had been threshed, prior to oats, flax seed appeared in several oat samples as far as the fourteenth oat bundle. It was impossible to clean this machine in any practical manner. Black barley grains appeared in the oat grain samples although no black barley had been

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[1]It must be noted here that Mr. Vogel was not responsible for the changes in this machine which made it undesirable from the standpoint of mixing grain.

threshed for three days of threshing prior to this test. The results in Table 5 indicate that mechanical mixing was undoubtedly an important factor in the impurity of oat varieties and selections which passed through this rod row thresher.

Tiller studies

It has been fairly easy to find individual Clinton plants whose various tillers do not reproduce progeny like the Clinton parent. When certain tall plants with open panicles ("lacy") were pulled, one or more tillers were sometimes found on the same plant which were shorter and had panicles of the typical Clinton type. By planting all panicles from a plant side by side in panicle rows, differences in their progenies could be observed and recorded.

Progenies from tall, "lacy" type panicles nearly always bred true for this type, and seldom gave any indication of producing Clinton-like progeny. One family of tall type plants was increased to several hundred panicle rows, none of which was like Clinton in strength of straw, height, or panicle type. All of these rows bred true for the tall type of the original tall tiller. One family was pure for white grains and was so much like Clinton that the grain color must have been due to mutation and not to other causes.

One particular Clinton plant produced four panicles. When planted in individual panicle rows, two were typical Clinton types, while the other two rows were of the tall type and both were susceptible to stem rust.

Table 5. Test of rod row nursery thresher to determine amount of possible mechanical mixing of oat varieties.

Order of threshing	Kind of grain threshed	Total weight of grain (Grams)	Number and kind of grain	Calculated number of mixed seeds per pound
1	Flax	—	—	—
2	Yellow oats	50	42 flax seed	381
			1 barley	9
3	"	45	4 flax seed	43
4	"	37	0	
5	Black oats	180	82 yellow oats	206
6	"	212	55 " "	118
			1 flax seed	2
7	"	204	53 yellow oats	118
			1 flax seed	2
8	Yellow oats	260	28 black oats	45
			1 flax seed	2
9	"	250	30 black oats	54
			1 flax seed	2
10	"	230	18 black oats	36
			2 flax seed	4
11	"	220	1 black oats	2
			2 flax seed	4
12	"	305	21 black oats	31
			1 flax seed	1
13	"	200	10 black oats	22
14	"	94	5 " "	24
			1 flax seed	5
15	"	50	3 " "	27
16	Black oats	316	54 yellow oats	78
			1 black barley	1
17	"	256	47 yellow oats	83
18	"	280	56 yellow oats	91
19	"	260	48 " "	83
20	"	265	28 " "	46
21	"	250	40 " "	72

Progenies from two panicles of a similar plant proved to be susceptible to both crown and stem rust, while their sister panicle progenies were resistant and resembled Clinton in every respect. A picture of these progeny rows is shown in figure 1. Rows grown from panicles taken from individual Clinton plants the previous season are shown in figures 2 through 10, inclusive.

Panicles of typical Clinton and the most common offtypes are shown in figure 11. The strong upright secondary branches of typical Clinton panicles were common, but when the tall plants were examined their panicles were found to have a characteristic drooping appearance to the secondary branches. The term "lacy" has been applied to these panicles to differentiate them from the typical Clinton panicles. Both types vary in the extent of their awn development, but are usually not awned, or only slightly awned.

Crosses were made between the tall type plants with lacy panicles and the typical Clinton plants. In several such crosses the parents traced back to panicles from the same plant the previous season, the principal differences being in their height and panicle type. In all of these crosses the tall plant type and "lacy" panicles seemed to be inherited as a dominant character.

Progeny testing

An important part of this study of variability in Clinton oats has been the progeny testing of 40 families, each of which originally traced

Fig. 1. Tiller progeny from the same Clinton plant. Rows 1 and 2 are typical Clinton rows. Rows 3 and 4 are tall, lacy off-type rows.

Fig. 2. Both panicle rows from a single Clinton plant of the previous season. Row 1 - Typical Clinton oats. Row 2 - Late maturing offtype.

Fig. 3. Tiller progeny from the same Clinton plant. Row 1 - Blue "bloom" to foliage, late maturing. Row 2 - Green foliage, late maturing. Row 3 - Green foliage, early maturing.

Fig. 4. Tiller progeny from the same Clinton plant. Row 1 - Typical Clinton. Rows 2 and 3 - Tall, lacy offtypes.

Fig. 5. Tiller progeny from the same Clinton plant. Row 1 - Tall, early, bronze kernels, susceptible to stem rust. Row 2 - Typical Clinton, yellow kernels, resistant to both rusts. Row 3 - Tall, early, bronze kernels, susceptible to both rusts.

Fig. 6. An uneven progeny all from the same plant. All three rows susceptible to crown rust.

Fig. 7. Tiller progeny from the same Clinton plant. Rows 1 and 3 - Later, susceptible to crown rust, yellow kernels. Row 2 - Tall, early susceptible to both crown and stem rust, bronze kernels.

Fig. 8. Tiller progeny from the same Clinton plant. Row 1 - Typical Clinton with excellent straw. Rows 2 and 3 - Tall, lacy, fair straw, susceptible to stem rust.

Fig. 9. Tiller progeny from the same Clinton plant. Rows 1 and 3 - Typical Clinton. Row 2 - Tall, lacy and susceptible to stem rust.

Fig. 10. Tiller progeny from the same Clinton plant. Row 1 - Typical Clinton. Rows 2 and 3 - Tall, lacy and susceptible to crown rust.

Fig. 11. Panicles from normal Clinton oats. Panicles from tall, lacy offtype Clinton.

back to one single panicle from Aberdeen, Idaho, in 1944. In figure 12 is shown the progeny nursery grown in 1946 to test the variability occurring in the 40 Clinton families. By this stage in the selection program all the variability due to mechanical mixtures and presumably most of that due to natural crossing had been removed, so that the remaining families were typical Clinton types except for tiller bud mutations which arose anew each generation.

A general view of the progeny nursery grown on the Agronomy Farm at Ames, in 1947, is shown in figure 13. Each long "range" was four feet wide and 360 feet long and contained 360 panicle rows. The three families which exhibited the least amount of variability in previous tests were increased to nearly 1,000 panicle rows each. The three families indicating the highest amount of variability in 1946 also were increased for observation in the 1947 nursery.

Five families of Bond and several of D67 and D69 also were increased and observed for their variability by the progeny method. None of these varieties were found to be pure and uniform. The rows of Bond varied in strength of straw, height, tillering ability and disease reaction. As previously mentioned, several plants were found in Bond which were resistant to stem rust. They were undoubtedly F_1 natural crosses with some other stem rust resistant variety. The D67 and D69 varieties were somewhat variable in maturity and height, although they were not as uneven as Bond.

Fig. 12. 1946 Clinton progeny nursery at Ames. 3,400 panicle rows.

Fig. 13. 1947 Clinton progeny nursery at Ames. 7,500 panicle rows.

Many panicle rows came from panicles picked at random from fields of the original unselected Clinton. When these were tested in progeny rows the percentage of offtype rows was considered a good indication of the total variability due to all causes. In figure 14 is pictured the tall, offtype panicles which appeared in considerable abundance in the Clinton variety. A few panicle rows from an uneven or variable Clinton family are shown in figure 15.

The frequency with which offtype plants appeared in the original Clinton variety is shown in Table 6. The offtype plants apparently

Table 6. Frequency of offtype panicle rows from original Clinton variety unselected since 1943 when grown in 1946 and 1947.

Location and year	Number of normal progeny rows	Number of offtype rows	Percentage of offtype rows
Ames, 1946	2,284	291	12.74
Ames, 1947	320	40	12.50
Kanawha, 1946	227	23	10.13
Kanawha, 1947	220	38	17.27

increased by mechanical mixing with other varieties, by natural crossing with other oats, and by tiller bud mutations until they occupied about 12 percent of the Clinton populations in 1947.

It was difficult in a study of this kind to assign definite percentage values to each cause of variability. In the first place, a clear-cut

Fig. 14. Tall, offtype plants as commonly seen in fields of Clinton oats.

Fig. 15. A few panicle rows from an uneven Clinton family, increased originally from a single panicle.

separation into the various causes of variability was difficult to make. It was probably impossible in many cases to determine if one offtype plant was due to natural crossing and another to a tiller bud mutation or to some other type of mutation. The figure of 0.25 percent was set in a previous section of this paper as the average percentage of annual natural crossing in Clinton, but the hybrids might have increased within the population faster than the self pollinated individuals. There was a strong indication that mechanical mixtures were an important source of variation in the Clinton population. Varietal mixtures also could vary in their competitive ability, disease reaction and yield and hence increase or decrease in the Clinton population over a period of several years. The variables in this problem were many, but certain studies were made to understand them better.

The frequency of offtype panicle rows for the three most uniform families is tabulated in Table 7. The most uniform family of the 40 studied in detail had only .04 percent offtype rows. The other two

Table 7. Frequency of offtype panicle rows from three of most uniform and highly selected Clinton families, 1947.

Family number	Number of normal progeny rows	Number of offtype rows	Percentage of offtype rows
10,007	1,950	20	0.10
10,015	952	4	0.04
10,021	915	12	0.13

uniform families contained relatively few offtype rows, but no family was found which was entirely free of mutant types. Probably the best that can be hoped for in a reselection of Clinton is to produce a strain with a minimum of tall, offtype plants. It may never be possible to select a pure line from the Clinton variety which will be completely uniform, but it should be possible, by the progeny testing method previously described, to find and increase certain families much better in their uniformity than the present Clinton variety.

An indication of the great spread of variability within the variety Clinton is shown in Table 8 which gives the frequency of offtype families selected for their non-uniformity. In certain families derived from the original Clinton it was difficult to find rows which did resemble Clinton.

Table 8. Frequency in 1947 of offtype panicle rows from two families originally selected in 1944 on basis of non-uniformity.

Family number	Number of normal progeny rows	Number of offtype rows	Percentage of offtype rows
10,025	85	145	63.04
10,050	0	130	100.00

In addition to the offtypes previously mentioned, a mutation of special interest in Clinton also was found. A panicle row in one of the most uniform families was found to be segregating for a chlorophyll deficient striping of the leaves. There appeared to be about three

plants with various degrees of striping to every one with normal green leaves. This row has not been progeny tested and, therefore, no genetic analysis can be given for this character.

Yield trial of Clinton families

The Clinton variety produced plants which varied in as many as twelve or more distinctly different morphological and pathological characters. The frequency of these aberrant types could be readily observed and recorded in short progeny row tests. The possibility existed that progeny rows which resembled Clinton in plant type might be significantly different in yield and test weight. Thirty-five selected families closely resembling Clinton in agronomic characters and a Clinton check were grown in a split plot replicated rod row yield trial at Ames in 1947. The sub-plots were five strains within each family. The data from this test are summarized in Tables 9 to 12, inclusive.

Clinton families ranged in yield from 60.6 to 70.4 bushels per acre (see Table 9). Twelve of these families yielded significantly higher than the Clinton check and none yielded significantly lower at the 5 per-cent level of significance.

The Clinton families ranged in average test weights from 37.5 to 34.8 pounds per bushel. There were eleven families significantly higher in test weight and three significantly lower than the Clinton check. There was a tendency for earlier maturing Clinton families to have lower average test weights in this experiment. There was a spread of approximately one week from the earliest to the latest family in the recorded date of heading.

Table 9. Adjusted mean yields, test weights and dates of heading of 35 Clinton families and a Clinton check grown in replicated rod rows at Ames, Iowa, in 1947.

Entry number	Family number	Adjusted mean yields in bu.	Test weights (pounds per bu.)	Date of heading in June
36	10,038	80.55	36.6	24
24	10,046	79.46	36.2	25
29	10,029	79.39	36.3	24
8	10,008	78.84	37.5	26
33	A-1812	78.56	36.2	24
16	10,016	78.32	35.3	24
27	10,027	78.14	36.8	25
18	10,015	77.98	36.5	24
26	10,026	77.96	37.4	25
25	10,049	77.59	37.0	24
31	A-1730	77.58	36.1	24
9	10,009	77.35	36.3	23
2	A-1368	76.96	37.3	26
15	A-1628	76.84	36.5	26
7	10,044	76.80	34.8	21
34	10,034	76.48	36.4	24
35	A-1823	76.46	37.0	24
3	A-1482	76.29	36.0	25
32	A-1782	76.18	37.2	24
21	10,015	76.17	36.9	24
5	10,042	75.94	36.0	22
17	10,007	75.77	36.3	25
28	10,028	75.48	37.3	25
13	10,045	74.71	37.0	24
22	10,027	73.64	36.8	25
11	10,011	73.60	36.4	25
6	10,043	73.39	35.5	25
19	10,019	73.21	37.2	24
23	10,036	73.14	36.2	24
30	10,030	73.04	37.4	25

Table 9 (Continued)

Entry number	Family number	Adjusted mean yields in bu.	Test weights (pounds per bu.)	Date of heading in June
1	Clinton (ck.)	72.95	36.3	24
10	10,010	72.76	36.1	23
4	10,041	71.98	36.0	25
14	A-1613	71.69	36.6	25
20	10,007	70.62	37.0	25
12	A-1497	70.36	36.5	25
	Means	75.73	36.5	24
	L. S. D. (5%)	4.22	.49	
	L. S. D. (1%)	5.58	.65	
	Coeff. Var.	10.95	11.80	
	Gain in Eff.	100.60	36.15	

The analysis of variance of yields and test weights given in Tables 10 and 11 indicates highly significant differences among the families in both of these characters.

After it was shown that the Clinton families differed significantly in both test weight and yield it seemed desirable to analyze the data further to determine if there were any differences between strains within families. Those families designated by numbers 10,007 to 10,049 consisted of five separate strains (within each family) each replicated six times. The remainder of the families, including the Clinton check, were represented by five rows from the same lot of bulk seed, each replicated six times. The analysis of variance was calculated separately as randomized blocks for each family; those represented by separate strains

Table 10. Analysis of variance of yields for 36 Clinton families grown at Ames in 1947 in a 6 x 6 triple lattice design with two groups of sets.

Source of variation	Degrees of freedom	Mean square
Replications	5	48,484.20
Comp. A.	(15)	15,282.33
Comp. B.	(15)	10,972.93
Blocks (Eliminating fam.)	30	13,127.63
Families (Ignoring blocks)	35	9,052.80**
Error (Triple lattice)	145	1,452.44
Error (Randomized blocks)1/	(175)	(3,453.90)
Within (Sampling error)	864	1,670.61

** Exceeds 1 percent level of significance when tested against error variance as randomized blocks.

Table 11. Analysis of variance of test weights for 36 Clinton families, 1947.

Source of variation	Degrees of freedom	Mean square
Replications	5	4.0940
Comp. A.	(15)	.8326
Comp. B.	(15)	.5673
Blocks (Eliminating fam.)	30	.7000
Families (Ignoring blocks)	35	2.1750**
Error (Triple lattice)	145	.1614
Error (Randomized blocks)1/	(175)	(.2540)

** Exceeds 1 percent level of significance when tested against error variance as randomized blocks.

1/ The complete analysis of variance as a randomized block design is not given, but the degrees of freedom and the appropriate mean squares for error are indicated for each table, to permit calculation of a valid F value.

as well as those represented by five samples of similar bulk seed, but will not be shown here in detail. A summary showing the yields by strains, the unadjusted mean yields and the F-values for each family are given in Table 12.

Significant differences at the 5 percent level among strains within families were indicated in four families from the twenty-six containing different strains. Among the ten families (nine from Aberdeen, Idaho, and one Clinton check) in which five samples of the same lot of seed were tested, none was significant at the 5 percent level. This would suggest that significant yield differences existed between strains within families. Further examination of the data show that in two of the families not represented by strains, the five samples tested closely approached the 5 percent level for significance. Obviously, no genetic differences should exist between these five lots from bulk seed. Therefore, there is some question whether a single year of testing has been sufficient to demonstrate conclusively that real differences actually exist among the strains.

An examination of the range in yield within families also shows that three of the families represented by bulk samples varied as widely as the four families represented by significantly different strains. Therefore, it would seem logical to assume that more critical tests are necessary before valid conclusions can be reached.

Table 12. Summary of mean strain and sample yields, unadjusted mean yields of families and F-values for strains and samples within families, 1947.

Entry number	Family number	Yields in bushels per acre: Strain or sample number 1	2	3	4	5	Unadjusted mean yields	F
17	10,007	74.3	74.0	76.3	72.2	75.6	74.5	.53
20	10,007	69.4	69.5	72.1	72.8	74.9	71.7	.81
8	10,008	81.0	79.0	81.2	78.9	75.1	79.0	.05
9	10,009	78.2	76.9	81.8	77.4	77.6	78.4	.30
10	10,010	73.3	70.7	68.2	72.3	76.5	72.2	1.11
11	10,011	72.4	74.4	71.1	64.7	73.4	71.2	1.89
18	10,015	81.8	79.7	76.0	81.3	83.0	80.4	1.04
21	10,015	75.3	83.3	72.2	75.7	77.1	76.7	2.52
16	10,016	77.0	74.8	80.0	74.3	74.7	76.2	.04
19	10,019	72.5	72.4	70.6	72.2	76.6	72.9	.94
26	10,026	76.0	74.7	74.6	74.9	80.1	76.1	.07
27	10,027	82.5	78.0	80.0	77.9	73.5	78.4	1.04
22	10,027	70.5	73.9	65.2	73.7	72.6	71.2	3.01*
28	10,028	71.9	70.8	79.3	73.2	72.7	73.6	.89
29	10,029	78.7	83.6	77.3	79.4	73.6	78.5	1.38
30	10,030	71.3	70.8	75.8	74.9	75.4	73.6	1.07
34	10,034	76.6	70.9	75.9	73.0	83.8	75.9	2.97*
23	10,036	69.1	72.8	67.1	77.6	75.5	72.4	4.42*
36	10,038	81.8	82.6	84.1	86.4	84.0	83.8	.03
4	10,041	72.0	70.0	67.0	63.0	75.5	69.5	3.74*
5	10,042	79.4	74.9	75.0	77.4	72.1	75.8	.73
6	10,043	75.3	70.8	70.6	74.1	75.7	73.3	.73
7	10,044	78.9	72.2	75.0	79.5	78.5	76.8	.98
13	10,045	78.8	73.9	71.9	76.0	79.5	76.0	1.34
24	10,046	82.4	81.1	82.3	81.2	81.4	81.7	.03
25	10,049	82.8	77.5	76.9	77.6	77.0	78.4	1.20
2	A-1368	74.8	74.3	73.9	77.7	81.9	76.5	1.09
3	A-1482	80.3	74.7	79.1	80.3	76.4	78.2	.45
12	A-1497	73.8	69.2	71.3	67.8	71.7	70.8	.88
14	A-1613	70.8	73.4	68.0	70.3	75.9	71.7	.48
15	A-1628	81.4	76.9	79.1	77.9	86.8	80.4	1.17

Table 12 (Continued)

Entry number	Family number	Yields in bushels per acre, Strain or sample number 1	2	3	4	5	Unadjusted mean yields	F
31	A-1730	74.7	72.0	74.6	78.9	84.1	76.8	2.85
32	A-1782	77.5	75.8	74.4	67.9	81.8	75.5	2.65
33	A-1812	81.7	81.3	80.4	81.0	80.0	80.9	.06
35	A-1828	75.3	73.4	73.7	76.3	78.5	75.4	.49
1	Clinton	70.6	73.0	70.0	71.4	73.0	71.6	.17

* Exceeds the 5 percent level of significance.

Cytological studies

As was pointed out previously, the Clinton variety is a selection from a species cross of A. sativa var. D69 x A. byzantina var. Bond. It is known that species crosses in other crop plants are often somewhat sterile and frequently quite unstable cytologically. Plant breeders had suspected that the same conditions might be true in Clinton oats.

Thousands of pollen counts using acetocarmine stain were made on many Clinton plants and none was found to have more than a trace of shrivelled, unstained pollen. Attention was then focused on the meiotic stages in microsporocytes of Clinton, its parents, and its progenies.

During the study of oat microsporocytes it was found impossible to interpret early prophase configurations. Under the conditions of fixing and staining used in this study the early prophase chromosomes exhibited an extreme tendency to shrink into a tight knot. It was not until late diplotene and diakinesis that the chromosome configurations were of much value, and then chiefly from the standpoint of counting chromosome numbers.

Metaphase stages in oat sporocytes were found to be of limited value from an analytical point of view. Anaphase figures were of value in discovering inversion bridges, lagging pairs and univalent chromosomes. The microspore quartet stage was useful for the identification and counting of micronuclei when they were present. Hence only three or four short stages in meiosis could be utilized in the cytological analysis of variability in Clinton oats.

In 1945 the cross D69 x Bond was remade in the greenhouse. Several F_1 plants were studied cytologically to determine the possible basis for the instability exhibited by Clinton. Chromosome counts at diakinesis in microsporocytes were relatively easy to make and revealed 21 pairs of chromosomes in practically all cases where complete counts were possible. No univalent, trivalent or quadrivalent associations were found and no micronuclei were in evidence in the several hundred sporocytes examined. The F_1 plants seemed to be quite regular in their meiotic behavior.

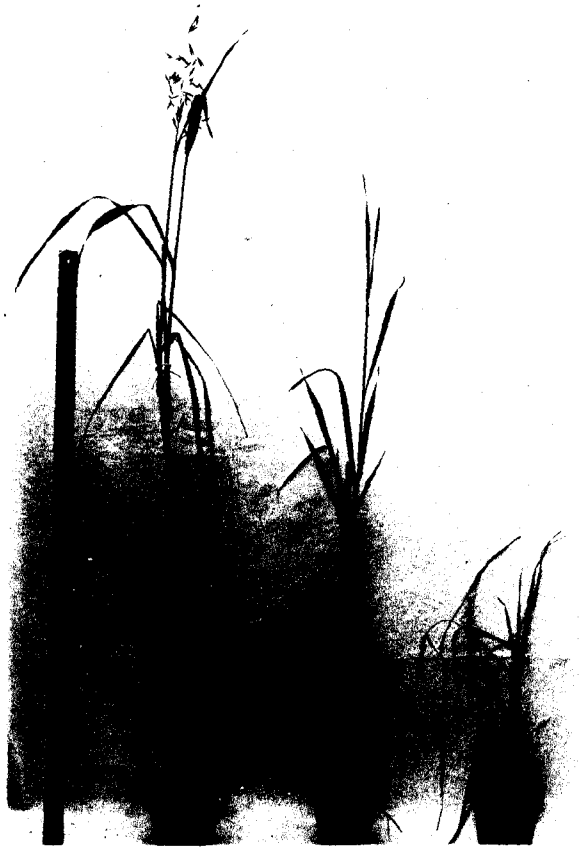
In the cross Bond x D67 the F_1 plants were regular at meiosis, with one exception. In this plant of Bond-J x D67-T, cytological irregularities were found in the F_1 and subsequent generations. The first irregularities noted were micronuclei in the quartets. They ranged from none to three or four per quartet member. When earlier stages were examined, the probable causes for the micronuclei were discovered.

At metaphase I, the members of one pair of chromosomes seemed to be widely separated from each other. Lack of homology was evident and

it is possible that synapsis did not occur. This pair of chromosomes was often seen to lie off the metaphase plate. The homologues seemed to be undergoing precocious anaphase movement, but this may be discounted, because during anaphase I they did not pass to their respective poles, but lagged behind the other chromosomes. In some figures the homotypic split was evident at anaphase I. The micronuclei found in some members of the quartet after anaphase II, indicated that most of these chromatids were left out of the nucleus. In later generations irregularities of this sort may lead to various offtype dwarf plants. Offtype progenies were not studied in detail but indications were that some of the plants were monosomic or nullisomic. Figure 16 shows the Bond-J parent on the left and the D67-T parent on the right as they grew in the greenhouse. Figure 17 shows the kind of plants obtained in the F_2 generation of Bond-J x D67-T. The first plant on the left in Figure 17 (a) is normal, (b) is a monosomic plant and (c) is a dwarf plant with undetermined chromosome number.

Studies on the meiotic chromosomes of Bond and certain pure line selections from this variety revealed some interesting cytological peculiarieties. In Bond-B-1, for example, about five percent of the microspore quartets were in linear order instead of the regular quartet or tetrad arrangement. In Bond-J one pair of chromosomes was precocious and traveled to the poles ahead of the others, while another pair tended to lag. The Bond-N selection and several others often had one or more pairs of chromosomes off the metaphase plate. This seemed to

Fig. 16. Bond-J parent. D67-T parent.



(a) (b) (c)

Fig. 17. F_2 plants of Bond-J x D67-T.
(a) Normal plant
(b) Monosomic plant
(c) Dwarf plant

be a common occurrence among chromosomes of even such apparently stable varieties as Richland and Cedar oats.

Several chromosome bridges were found in various Bond selections. Such bridges suggest that the plant under observation was heterozygous for at least one inverted chromosome segment. The persistence of this condition is difficult to explain in Bond and other oat varieties, and in self pollinated plants generally. After several years self pollinated lines should be reasonably homozygous for either the normal chromosome pair or the inverted chromosome pair. Theoretically the inversion heterozygotes should be eliminated as rapidly as any other heterozygotes in an inbred population.

Golden Rain, one of the parents of Bond, was examined cytologically and found to be regular in bivalent associations and anaphase divisions. Chromosomes at diakinesis in a microsporocyte of Golden Rain are shown in figure 18. Twenty-one pairs of chromosomes can readily be counted. For the other parent of Bond, A. sterilis gulta var. Red Algerian, the exact strain was not obtained, and consequently could not be examined cytologically. A closely related type, C.I. 840, was perfectly regular in the limited observations of its microsporocytes.

The D67 and D69 varieties were examined rather carefully and found to be quite normal cytologically.

Meiosis in Benton oats, a selection from a cross of D69 x Bond, was regular so far as the study was carried, although only a relatively small number of sporocytes were examined. A diakinesis figure of Benton oats is shown in figure 19.

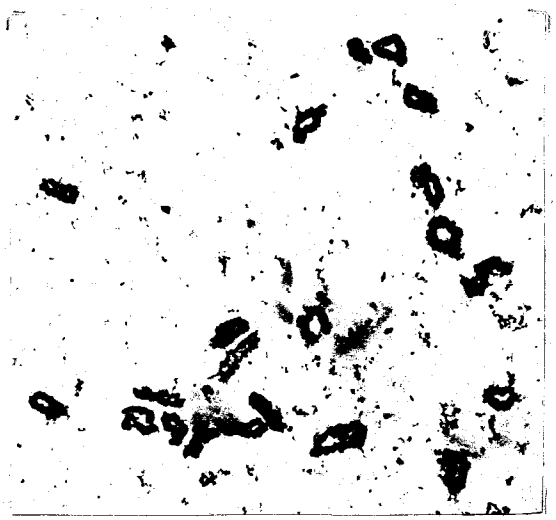


Fig. 18

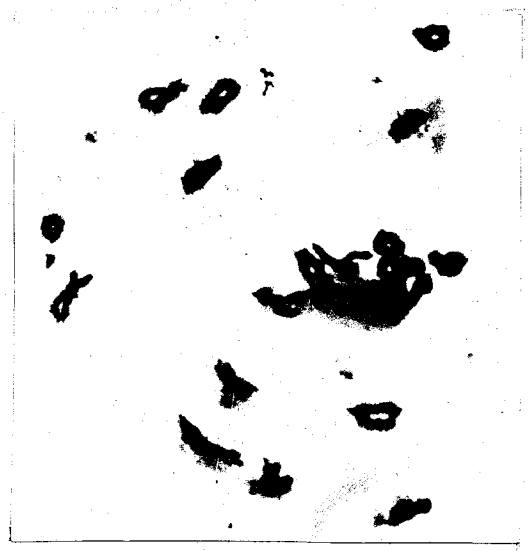


Fig. 19

Figure 18 - Twenty-one normal bivalent chromosomes in Golden Rain oats, one of the parents of Bond.

Figure 19 - Twenty-one normal bivalent chromosomes in Benton oats, a Clinton sister selection.

When typical Clinton plants were examined cytologically twenty-one bivalent chromosomes were found consistently at diakinesis; frequently accurate counts of the groups of 21 could be made at anaphase I. Figures 20, 21 and 22 show sporocytes from typical Clinton plants with twenty-one pairs of chromosomes at diakinesis.

Bond plants regularly showed twenty-one pairs of chromosomes at diakinesis as in figures 23 and 26. Occasionally trivalent associations were found in certain offtype Clinton plants. A trivalent association with a univalent just above the group of three chromosomes can be seen on the left in figure 24. Certain plants in the F_2 generation of Bond-J x D67-T, when observed cytologically, gave monosomic microsporocytes as seen in figure 25, page 58. In this figure there are twenty pairs of chromosomes plus a univalent chromosome, giving a total of only forty-one somatic chromosomes instead of forty-two for this particular plant.

Several offtype plants were found in the Clinton variety which gave indications of cytological irregularities. The diakinesis stage from a microsporocyte of such a plant is shown in figure 27. The arrow in the photograph points to a possible univalent or heteromorphic chromosome. Other chromosomes in this cell were paired regularly.

Some metaphase I chromosome arrangements are shown in figures 28, 29 and 30. At least one open bivalent chromosome can be seen in figure 28, and an open and a closed bivalent are quite evident in figure 30. Two chromosomes in figure 29 were characteristically apart at metaphase I in F_2 plants of the cross Bond-J x D67-T (see figure 17), and most certainly contributed to micronuclei and loss of chromatin in those plants.

Figures 20, 21 and 22 - Twenty-one normal bivalent chromosomes in typical Clinton oats. Notice the internal spirals of chromosomes in figure 21. Size differences also can be observed in the Clinton chromosomes.

Figure 23 - Twenty-one normal bivalent chromosomes in Bond oats. Arrow points to remnants of the nucleolus.

Figure 24 - Microsporocyte in which chromosome pairing is abnormal. To the left a trivalent association with a univalent chromosome just above it can be seen. The plant under observation was an offtype selected from Clinton.

Figure 25 - Microsporocyte showing twenty pairs plus one univalent chromosome. This plant was from an F_2 progeny of a Bond-J x D67-T cross which produced many dwarf and irregular type plants.

Figure 26 - Twenty-one pairs of chromosomes at diakinesis in Bond oats.

Figure 27 - Chromosomes from microsporocyte of offtype Clinton oats showing twenty pairs of chromosomes plus a univalent chromosome or a heteromorphic chromosome pair. (see arrow).

Figure 28 - Metaphase figure from an offtype Clinton plant showing at least one open bivalent chromosome.

Figure 29 - An open pair of chromosomes at metaphase, which probably never synapsed in prophase stage. This microsporocyte was from an F_2 plant of Bond-J x D67-T. The chromosomes pictured apart often split homotypically at anaphase I and were responsible for micronuclei as shown in figure 32.

Figure 30 - Metaphase figure from an offtype Clinton plant showing one open bivalent and one closed pair away from the metaphase chromosome group.

Fig. 20

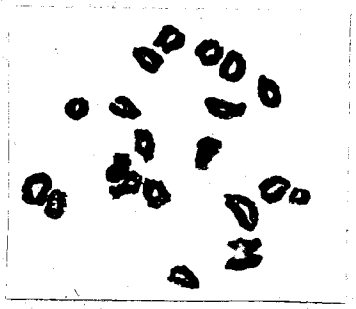


Fig. 21

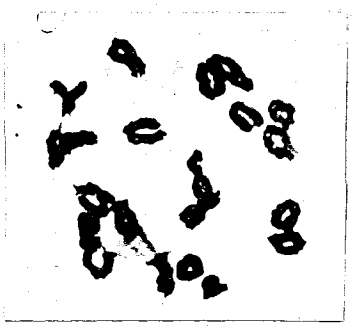


Fig. 22

Fig. 23

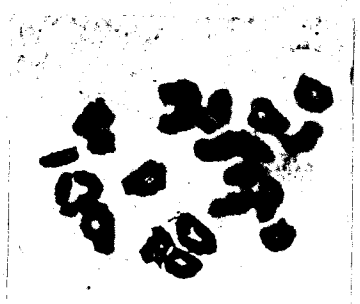


Fig. 24

Fig. 25

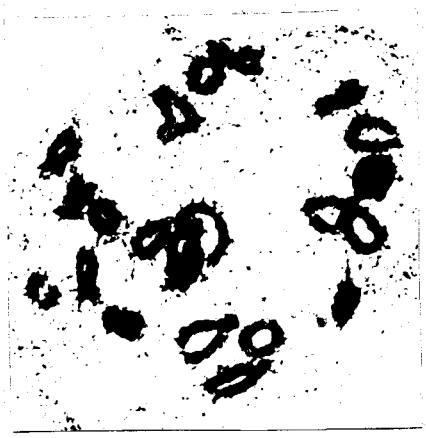


Fig. 26

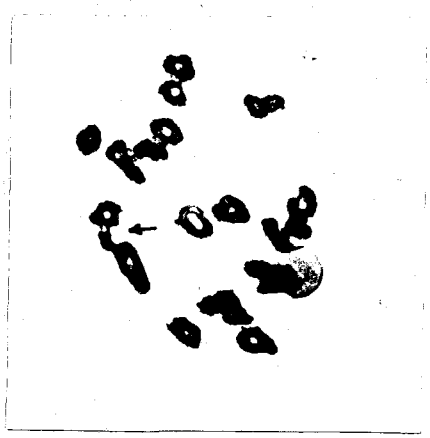


Fig. 27

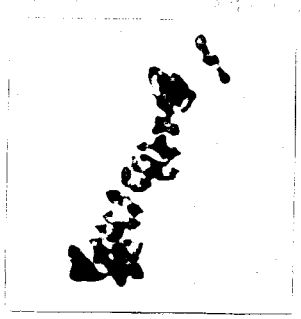


Fig. 28

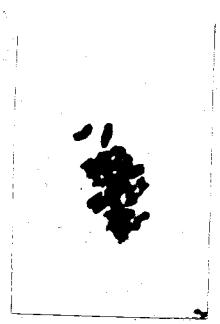


Fig. 29

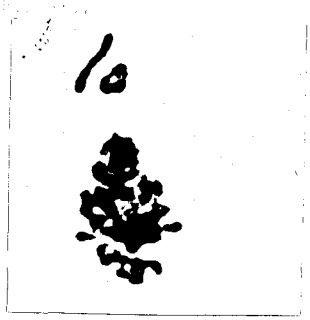


Fig. 30

Lagging chromosomes in two separate cells at anaphase I can be seen in Figure 31. Sometimes univalent chromosomes split homotypically at this stage and then wandered at random, forming micronuclei at the tetrad stage as shown in Figure 32.

Various types of bridges and stretching and breaking of chromatids under tension can be seen in Figures 33, 34, 35 and 36. A double chromatid bridge is evident in Figure 35.

The number of anaphase I bridges observed in offtype progenies of Clinton, in a few Clinton pure lines, and in parents and grandparents of Clinton are recorded in Table 13. It will be noted that bridges were most frequently observed in the Bond parent and in certain Clinton off-types. In these preliminary cytological observations no anaphase bridges were found in typical or uniform Clinton progeny.

Very often the orientation of pairs at the meiotic metaphase plate was not regular in plants of true-type Clinton. Sometimes more than 50 percent of the sporocytes had one or more pairs of chromosomes off the metaphase plate. This condition seems to be common in many oat varieties. No correlations were found between this character and the morphology or pathology of the progeny plants. In other words, chromosome pairs off the metaphase plate probably mean very little as regards variation in oats, unless they contribute to a loss in chromatin.

Figure 31 - Two cells at anaphase I showing lagging chromosomes. These microsporocytes were taken from an offtype Clinton plant.

Figure 32 - Micronuclei in quartets of an F_2 plant from the cross Bond-J x D67-T. This cross produced many dwarf and offtype plants.

Figure 33 - Broken chromatid strands at anaphase I in a tall type Clinton plant.

Figure 34 - Broken and attenuated chromatid strand in an offtype Clinton plant.

Figure 35 - Double chromatid bridge at anaphase I in an offtype Clinton plant.

Figure 36 - Attenuated and broken chromatid strands in a microsporocyte of an offtype Clinton plant.

Fig. 31

Fig. 32

Fig. 33

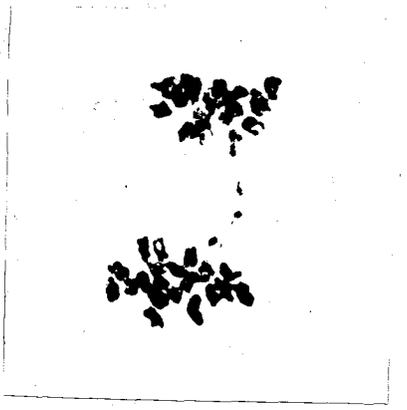


Fig. 34

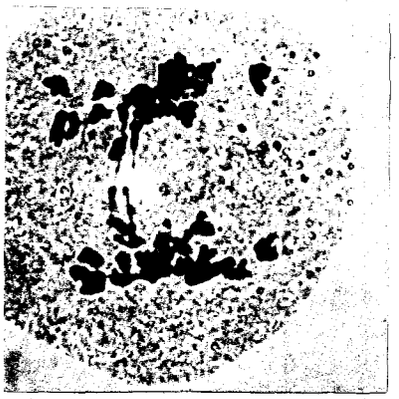


Fig. 35

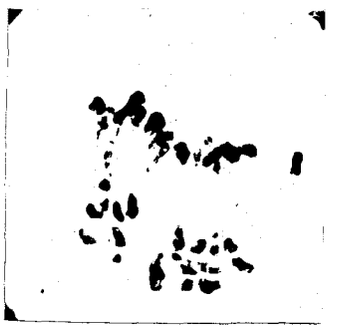


Fig. 36

Table 13. Frequency of inversion bridges at meiosis in certain oat selections and varieties.

Variety	Number of sporocytes with: No bridges	Single bridge	Double bridge	Percentage of bridges
A. sterilis maximina	58	0	0	00
A. sterilis culta, C.I.-840	134	0	0	00
Golden Rain	69	0	0	00
D69	167	0	0	00
D67	89	0	0	00
Benton	49	0	0	00
Bond B-2	91	1	0	1.08
Bond C	225	0	0	00
Bond J	139	1 †	0	.71
Bond N	56	2	4 *	9.67
Bond S	101	3	0	2.88
Clinton 220-1 (normal)	111	0	0	00
" 4321 "	113	0	0	00
" 4351 "	125	0	0	00
" 221-1 (off-type)	35	0	0	00
" 3 "	62	0	0	00
" 4 "	70	0	0	00
" 5 "	62	2	0	3.12
Clinton 222-1 "	100	0	0	00
" 2 "	64	2	0	3.03
" 3 "	29	0	0	00
" 5 "	111	1 **	0	.89
Clinton 139-1 "	58	0	0	00
" 2 "	16	0	0	00
" 3 "	81	0	0	00
" 4 "	40	0	0	00
" 140-3 "	114	0	0	00
" 141-1 "	26	0	0	00
" 2 "	15	0	0	00
" 3 "	43	2	0	4.44
Clinton 4321 "	110	7	0	5.98
" 4331 "	91	4	0	4.21

* One double bridge at anaphase II.
** A bridge with a visible acentric fragment.

DISCUSSION

Somatic mutations causing tiller differences with so great a frequency as found in Clinton oats are difficult to explain. No data bearing upon the actual cause of changes in the tiller buds were obtained in this study. However, it has been established that these changes or mutations do apparently take place in somatic tissue and not at meiosis. The mutations were not in the nature of a gain or loss of an entire chromosome, or even the loss or gain of an arm of a chromosome. Cytological evidence substantiates these statements. The changes in morphological and pathological characters cannot possibly be due to physiological changes within the plant; these changes in characters must have a genetic basis.

Any hypothesis which seeks to explain tiller differences must take into account the specific, directional and seemingly irreversible changes found in tall tillers. Somatic crossing over will probably most readily explain the tiller differences found in the Clinton variety. There are two ways in which somatic crossing over might occur, (1) between homologous chromosomes or (2) it might occur between non-homologous chromosomes of the complement.

If it is presumed that the cross overs occur between homologous chromosome pairs in a self pollinated crop such as oats, it is difficult to explain how this could cause any differences in the phenotypes. In a homozygous plant the paired loci of homologous chromosomes should be identical, and a somatic cross over would never be detected.

There is the possibility, however, that the cross over might occur at different loci levels of the homologous chromosome pair. If the spindle fiber points of homologous chromosomes are not opposite each other and a cross over occurs, a bridge and fragment could be produced in a later somatic anaphase. A deletion of this type from the daughter cell of a new tiller bud could conceivably produce an offtype tiller.

It might also be assumed that cross overs could occur between semi-homologous or non-homologous chromosomes in somatic tissue. In other organisms tendencies for crossing over have been definitely established for specific arms of particular chromosomes. For hypothetical purposes such an assumption could be made to explain tiller differences.

It could be supposed that semi-homologous chromosomes A* and X of Clinton oats are heterozygous for a small inverted portion. If one of the somatic chromosomes from pair A and one from pair X cross over within the inverted region a fragment, a dicentric chromatid and two normal chromatids could be formed at somatic anaphase. If the fragment (which would be lost) carried inhibitor genes for tallness and lacy panicle types, the tiller resulting from such a deficiency would be taller than Clinton and have a lacy panicle. However, the daughter cell would be heterozygous for this deletion because the homologous chromosome mate would not be deficient. It is difficult from this standpoint to explain

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* An arbitrary designation

why tall types breed relatively true for the tall, lacy types and never produce Clinton-type progenies. By random recombinations of eggs and sperms at fertilization about one typical Clinton plant should be produced for every three tall types.

To assume differential fertilization would probably be to assume too much without more experimentation. Neither could it be logically expected that both homologous chromosomes would have the same deficiencies or duplications at the same time. Tiller differences would be equally difficult to explain by duplications, translocations or other similar mechanisms. Since a three to one ratio is not obtained in the next generation, the mutation causing tall types is probably not a simple one.

It is difficult to imagine the genes for stem rust, crown rust, hale blight, panicle type, height and various other factors all located in a single chromosome pair. If these factors are located on several chromosomes it is still more difficult to explain how they could mutate simultaneously to cause the multiple changes observed in Clinton offtypes.

Before leaving the subject of tiller bud mutations the possibility of "position effects" should be mentioned. Perhaps the tall types from Clinton are the result of "position effects" after somatic chromosomal rearrangements. This phenomena has been shown to operate in Oenothera and in some species of insects. At present much more study would be necessary to show that "position effects" have anything to do with Clinton variability, but all possible reasons for variability should be mentioned. As stated before, any explanation of tiller differences must take into

account the directional and seemingly irreversible nature of tall, lazy type plants in Clinton oats.

Because of the great range of variability among Clinton families, and the possibility of selecting families which may maintain themselves at a given mutation rate, a genetic basis for the rate of mutations is suggested. Evidence of a graded series of mutation rates among the families (from high to low) would indicate that the mutations are influenced or perhaps controlled by genetic factors. If genetic factors do control variability in Clinton oats they may be of a multiple nature. It also should be possible to obtain more uniform families from Clinton by selecting the proper genotypes, provided the inheritance of variability is on a genetic basis.

Another intangible part of this study was the appearance of bridges in pure line selections of Bond, and similar evidence of inversion heterozygotes in the offtype Clinton plants. There is either a natural selection in favor of the survival of inversion heterozygotes, or they are produced anew each generation. Natural crossing might conceivably account for a few inversion heterozygotes, but this could be eliminated in experimental material by bagging the oat panicles with glassine bags.

Pairing of semi-homologous chromosomes (allosyndesis) might be the reason for the appearance of inversion bridges following crossing over within an inversion at meiosis. Instead of always pairing with their mate some chromosomes might pair with other chromosomes which have homologous sectors in common.

It is hoped that the present study has answered the pressing problems on the extent of variability in Clinton oats and will serve to indicate the nature of the variability. Much more work will be necessary to find the exact somatic mechanism which operates to give tiller variability in Clinton oats.

The stages for a critical study of meiosis in oat sporocytes are so limited that somatic studies should be attempted using root tips and very young tiller buds with appropriate staining methods.

SUMMARY AND CONCLUSIONS

1. Natural crossing occurs in Clinton oats on the average of about 0.25 percent and will account for a portion of the variability in the Clinton variety.

2. Mechanical mixing has undoubtedly been responsible for a portion of the variability found in Clinton.

3. The total variable plants found in a Clinton population usually average about 12 percent due to all causes. Tiller bud mutations account for the greatest share of this variability, while natural crossing and mechanical mixtures are responsible for a smaller share of the variability.

4. Tiller differences are thought to be due to somatic chromosome changes (mutations) which take place in the early ontogeny of the young tiller bud. Somatic crossing-over between semi-homologous chromosomes may bring about the chromosome rearrangements necessary to produce (a) small deletions or duplications not cytologically evident, or (b) position effects.

5. Panicles taken from the same individual Clinton plant have repeatedly been shown to differ in their breeding behavior. Differences between tillers on the same individual plant are often shown in type of panicles, height of tillers, disease resistance and other characters.

6. Tall type plants with open, "lacy" panicles are the most common offtypes in Clinton populations. They are often susceptible to crown and stem rust, and usually have weaker straw than Clinton.

7. Tall type plants breed relatively true for the tall, "lacy" type. Some segregation may be observed in progenies of tall plants, but they never produce progenies which completely resemble typical Clinton oats.

8. The tall type is inherited as a dominant character.

9. Clinton produces plants which may vary in as many as twelve or more morphological and pathological characters.

10. Clinton progenies also have been shown to differ significantly in their test weights and yielding abilities. Four out of thirty-six families showed significant differences in yielding ability among strains within families.

11. It is possible to reselect within the Clinton variety and eliminate the variability due to natural crossing and mechanical mixtures.

12. Most important of all, it is possible to select by the pedigree method, uniform families from the Clinton variety which will breed relatively true.

13. The Clinton variety of oats is a selection from a cross between two oat species, A. sativa and A. byzantina. These two parental species apparently have been differentiated in nature so long that their chromosomes are no longer entirely homologous.

14. Tall types are not cytologically stable. Inverted chromosome segments are present as indicated by inversion bridges in microsporocytes. Occasionally trivalent and univalent chromosomes as well as micronuclei also may be found.

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ACKNOWLEDGMENTS

The writer wishes to express his sincere appreciation to Dr. I. J. Johnson and to Dr. H. C. Murphy who gave him assistance with the agronomic, pathologic and genetic aspects of this problem; and to Dr. J. E. Sass for his assistance with the cytology and photomicrography. The writer also wishes to extend his most sincere thanks to the many other people who gave him new ideas and encouragement, and especially to those who actually helped with the mechanics of this extensive project. Thanks also are extended to Mr. John Staby who took the general photographs.